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REVISION OF *CHAPTALIA* (ASTERACEAE: MUTISIEAE) FROM NORTH AMERICA AND CONTINENTAL CENTRAL AMERICA

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ABSTRACT

Based on field and herbarium study, a revisionary study is presented for the species of *Chaptalia* from North and continental Central America. Six species comprise sect. *Chaptalia*; two of these are newly described, **C. estribensis** Nesom and **C. madrensis** Nesom, both from eastern México. Species of sect. *Chaptalia* are characterized by central flowers with sterile ovaries and ligules with purple midstripes and are restricted to México and the southeastern United States. The remaining six species in the present treatment belong to other sections of *Chaptalia* centered primarily in South America. Typifications are clarified for *C. pringlei*, *C. tomentosa*, and *C. nutans*; the application of the names *C. petrophila* and *C. spathulata* remains somewhat uncertain. The proper disposition of *Chaptalia lyrata* D. Don requires that a new combination be made for it, ***Leibnitzia lyrata*** (D. Don) Nesom, which supplants the name previously used for the same species, *Leibnitzia seemannii*.

KEY WORDS: *Chaptalia*, *Leibnitzia*, Mutisieae, Asteraceae

Chaptalia comprises about 56 species, the genus ranging widely through South America into Central America and México; one large group of species is endemic to the West Indies; a single species (*C. tomentosa* Vent.) is somewhat isolated in the southeastern United States, its closest relatives among the Mexican species. The generic boundaries between *Chaptalia* and the primarily Old World genera related to it (particularly *Gerbera* L. and *Leibnitzia* Cass., see Jeffrey 1967) are problematic. The two New World species of *Leibnitzia* (Nesom 1983) have previously been regarded as congeneric with *Chaptalia*.

The only large-scale study of *Chaptalia* (Burkart 1944) concentrated on Argentine species and provided only a synoptical treatment for the remainder of the taxa. Burkart listed 53 species; after additions and significant taxonomic realignments since Burkart's study, I find evidence for roughly the same number of species. Since 1944, six taxa have been replaced or transferred to *Chaptalia* from *Trichocline* (Zardini 1975; Cabrera 1973) and four new species have been described from South America (Cuatrecasas 1961, 1965).

Treatments of *Chaptalia* species from North America (Vuilleumier 1969; Simpson 1978; Cronquist 1980) have been limited in scope, and Central American studies (Simpson 1975) also have dealt with only a few species. Many endemic taxa have been described from the West Indies and the genus in that area is in need of study and

summary. Five taxa in Burkart's account of *Chaptalia* have been consolidated as a single species and transferred to the genus *Leibnitzia*. Finally, two new species of *Chaptalia* and a number of synonyms are recognized for the first time in the present study, which provides a systematic treatment of *Chaptalia* from North and continental Central America.

Field observations of eleven of the twelve species of *Chaptalia* recognized in the present study have provided valuable insights into species delimitations and relationships; I have not seen *C. albicans* (Sw.) Vent. *ex* Steudel or the problematic populations identified as *C. spathulata* (D. Don) Hemsl. and *C. petrophila* Greene. Simpson (1975, p. 1277) observed that "many specimens seem to intergrade between species," but the only instance where I have observed the possibility of such intergradation is between *C. nutans* (L.) Polak. and *C. texana* Greene, as discussed below. Because of their relatively simple habit (a rosette of basal leaves with scapose, monocephalous stems), the species of *Chaptalia* are superficially similar among themselves.

Specimen citations below are abbreviated in most cases, the distributional data provided by the maps; fuller specimen information is on file in the *Chaptalia* reprint folder at TEX.

CHAPTALIA Vent., *Descript. Pl. Nouv. Jard. Cels* 61. 1802. TYPE: *Chaptalia tomentosa* Vent.

Leria DC., Ann. Mus. Natl. Hist. Nat. 19:68. 1812. (*non* Adanson 1763.). *Chaptalia* sect. *Leria* (DC.) Burkart, Darwiniana 6:560. 1944. TYPE: *Leria nutans* (L.) DC., based on *Tussilago nutans* L. (= *Chaptalia nutans* [L.] Polak.).

Lieberkuhna Cass., *Dict. Sci. Nat.* 26:286. 1823. *Chaptalia* sect. *Lieberkuhna* (Cass.) Burkart, Darwiniana 6:539. 1944. TYPE: *Lieberkuhna bracteata* Cass., *nom. illeg.*, based on *Perdicium piloselloides* Vahl (= *Chaptalia piloselloides* [Vahl] Baker).

Loxodon Cass., *Dict. Sci. Nat.* 27:253. 1823. *Chaptalia* sect. *Loxodon* (Cass.) Burkart, Darwiniana 6:534. 1944. TYPE: *Loxodon brevipes* Cass., *nom. illeg.*, based on *Tussilago exscapa* Pers. (= *Chaptalia exscapa* [Pers.] Baker).

Oxydon Lessing, Linnaea 5:357. 1830. TYPE: *Oxydon bicolor* (Willd. *ex* Less.) Lessing, *nom. illeg.*, based on *Chaptalia runcinata* Kunth.

Thyrsanthema Necker *ex* O. Kuntze, *nom. superfl. illeg.*, *Rev. Gen. Pl.* 1:369. 1891. *Thyrsanthema* Necker, *nom. illeg.*, *Elem.* 1:6. 1790. LECTOTYPE (Kuntze 1891, but see comments below): *Thyrsanthema nutans* (L.) O. Kuntze (= *Chaptalia* [*Tussilago*] *nutans* [L.] Polak.). Necker's proposed generic name was provided with a Latin description but not with the citation of any species or any indication of a type; he mentioned only the Linnaean genus *Tussilago*. *Thyrsanthema* was not validated until 1891 by O. Kuntze (*Rev. Gen. Pl.* 1:369.); indications in various literature that *Chaptalia* is a conserved name apparently are based on the mistaken assumption that it was predated by Necker's *Thyrsanthema* (see comments by Rickett & Stafleu 1960). In contrast to Kuntze, Greene (1906) observed that the best choice for the lectotype of *Thyrsanthema* should not have been the monocephalous *Tussilago nutans* but rather some thyrsiflorous species of *Petasites*, which Linnaeus reduced to *Tussilago*. Correspondingly, in what amounts to an alternative lectotypification, Greene suggested that *Petasites* (*Tussilago*) *hybridus* (L.) Gaertn., Mey., & Scherb. is closer to Necker's intended application of

Thyrsanthema and made the nomenclatural combination as *Thyrsanthema hybrida* (L.) Greene (Leafl. Bot. Observ. 1:158. 1906.).

Perennial herbs, sometimes with a short rhizome, producing numerous, thick fibrous roots, a rosette of basal leaves, and monocephalous, bracteate or ebracteate scapes. Leaves elliptic to obovate, entire to toothed or lobed, sometimes lyrate, usually densely appressed-villous beneath, often glabrous or glabrescent above. Heads cylindrical to campanulate, erect at anthesis but either nodding or erect in bud and again in fruit; receptacles flat to shallowly convex, foveolate to smooth. Flowers dimorphic or trimorphic in 2-3 concentric zones, one zone of the pistillate flowers lacking when dimorphic. Outer flowers pistillate in 1-2(-3) series, the corollas ligulate, with or without a bifurcate inner lip, creamy-white to purple; corollas of the inner pistillate zone with a reduced ligule and inner lip, sometimes reduced to only the style and tube; style branches terete and linear to flattened and oblong. Innermost flowers bisexual, sometimes with sterile ovaries, the corollas bilabiate with recurved or coiling lobes, sometimes nearly regular with shallow lobes. Achenes fusiform, often slightly flattened, with or without a constricted neck or long beak, mostly 4-12 ribbed, glabrous or with short, inflated duplex trichomes with rounded to minutely apiculate apices; pappus bristles more than 50, minutely barbellate. Base chromosome number, x=24.

The inner pistillate flowers of *Chaptalia* appear to be transitional between the ligulate, outer, pistillate ones and the tubular, inner, bisexual flowers in two ways: 1) they usually are bilabiate, even if the outermost are not, and 2) in some species they sporadically produce small, abortive stamens. In none of the North and Central American *Chaptalia*, however, are these "staminodia" as large or well-developed as in the species of Old World genus *Gerbera*, where they have been used as a diagnostic character to separate the two genera (Burkart 1944; Zardini 1974).

SECTIONAL TAXONOMY

The species of *Chaptalia* were divided by Burkart (1944) into seven sections. These appear to be natural groups after the admission of several caveats (comments below). Six of the North and Central American species constitute sect. *Chaptalia*; five are members of sect. *Leria*, and one belongs with sect. *Lieberkuhna*. Sect. *Archichaptalia* Burkart and sect. *Pseudotrichocline* Burkart are confined to South America, and sect. *Microchaptalia* Burkart, which appears to be morphologically heterogeneous, is endemic to the West Indies.

Chaptalia section *Chaptalia* (species 1-6)

Scapes ebracteate (bracteate in one species), heads nodding in bud, bisexual flowers with sterile ovaries, and relatively broad ligules with a purple, abaxial midstripe. Sect. *Chaptalia* is a clearly monophyletic group of six species in México and the southeastern United States. *Chaptalia tomentosa* (southeastern U.S.) and *C. madrensis* Nesom (Sierra Madre Oriental of México) appear to be specialized within the section in their narrowly beaked achenes and pistillate ligulate corollas without an inner lip. The pattern of geographic disjunction between these apparent sister species also is found in numerous other taxa of plants and animals (*e.g.*, Rosen 1978). *Chaptalia lyratifolia* Burkart, *C. estribensis* Nesom, and *C. hintonii* Bullock are similar

in their strongly colonial habit from long rhizomes, leaves with cordate bases and strongly mucronulate margins, pistillate flowers with markedly foreshortened style branches, and unbeaked achenes. Among these, *C. lyratifolia* and *C. estribensis* produce thick-coriaceous leaves and probably are most closely related to each other. *Chaptalia pringlei* Greene is relatively isolated within the section: the stems usually are bracteate, the heads lack a zone of eligulate pistillate flowers (all pistillate flowers are distinctly ligulate) and the achenes produce a short, slightly constricted neck.

Chaptalia section *Leria* (DC.) Burkart (species 7-11)

Scapes bracteate or ebracteate; heads nodding in bud; central flowers with fertile ovaries; and ligules narrow, without a midstripe. Jeffrey (1967) suggested that sect. *Leria* be combined with sect. *Lieberkuhna*, but I agree with Burkart (1969) the two groups are distinct. *Chaptalia nutans* and *C. texana* appear to be closely related to each other; the phyletic affinities of *C. hololeuca* Greene, *C. transiliens* Nesom, and *C. albicans* are unclear. The scapes of *C. albicans* are prominently dilated just beneath the heads, a feature found in some species of sect. *Microchaptalia*.

Chaptalia section *Lieberkuhna* (Cass.) Burkart (species 12)

Scapes bracteate, heads erect in bud, central flowers with fertile ovaries, and the heads alternating between chasmogamous and cleistogamous modes. As noted by Burkart (1969), the monotypic sect. *Loxodon* (Cass.) Burkart almost certainly belongs with this group. Taxa now treated as *Leibnitzia* are excluded from sect. *Lieberkuhna* sensu Burkart. *Chaptalia runcinata* Kunth is morphologically isolated in North America; its closest relatives are the five other South American species of the section.

ARTIFICIAL KEY TO THE *CHAPTALIA* SPECIES OF NORTH AMERICA AND CONTINENTAL CENTRAL AMERICA

1. Scapes with 1-8 bracts.....(2)
1. Scapes ebracteate.....(4)
   2. Leaf blades subcoriaceous; heads 5-8 mm wide (pressed), erect in bud; phyllaries glabrous or subglabrous; disc corollas 5.2-6.2 mm long; achene body glabrous except for carpopodial papillae.....*C. runcinata*
   2. Leaf blades herbaceous; heads 8-20 mm wide (pressed), nodding in bud; phyllaries villous; disc corollas 7.5-9.7 mm long; achene body densely papillose at least on the neck.....(3)
3. Leaf bases attenuate; heads with only one series of pistillate flowers, these prominently ligulate and with sparsely pubescent tubes; achenes papillate only on the neck.....*C. pringlei*
3. Leaf bases cordate; heads with an inner series of pistillate flowers with ligules absent or greatly reduced and with glabrous tubes; achenes papillate over the whole surface.....*C. hintonii*
   4. Pistillate flowers in a single series, these prominently ligulate and with sparsely pubescent tubes.....*C. pringlei*
   4. Pistillate flowers in two series, those of the inner with ligules absent or greatly reduced; ligulate corollas glabrous.....(5)
5. Plants commonly interconnected by rhizomes, strongly colonial; leaf bases strongly cordate, with or without lyratiform extensions below.....(6)

5. Plants solitary; leaves often lyrate, the bases attenuate to truncate, if cordate then weakly so. ..... (8)
   6. Leaf blades thin-herbaceous, sometimes reddish. ..... *C. hintonii*
   6. Leaf blades thick-coriaceous, never reddish. ..... (7)
7. Leaf blades often lyrate; ligulate flowers 12-25. ..... *C. lyratifolia*
7. Leaf blades abruptly cordate, never with lyrauform extensions; ligulate flowers 24-35. ..... *C. estribensis*
   8. Leaves elliptic, the bases attenuate; heads erect in bud, flower, and fruit; peduncles prominently dilated beneath the heads; ligules 0.2-0.3 mm wide. ..... *C. albicans*
   8. Leaves elliptic to lyrate, the bases attenuate to truncate; heads nodding in bud and fruit; peduncles not dilated below the head; ligules 0.2-2.0 mm wide. ...(9)
9. Flowers trimorphic or ligulate pistillate flowers lacking and then flowers dimorphic; ligules 0.2-0.8 mm wide; disc corollas nearly regular with short, erect corolla lobes; achenes 11.5-16.6 mm long. ..... (10)
9. Flowers trimorphic, ligulate pistillate flowers always present; ligules 0.8-2.0 mm wide; disc corollas bilabiate with prominent, coiling or recurved lobes; achenes 3.5-11.2 mm long. ..... (11)
   10. Leaves thin-herbaceous when dry; rhizome often absent; phyllaries 15-25 mm long at achene maturity; style branches of pistillate flowers 0.7-1.3(-1.5) mm long; achene body 0.6-0.8 mm wide. ..... *C. nutans*
   10. Leaves distinctly thickened when dry; lateral rhizome present; phyllaries 14-18 mm long at achene maturity; style branches of pistillate flowers (1.0-)1.6-2.3 mm long; achenes body 0.8-1.0 mm wide. ..... *C. texana*
11. Leaves mostly panduriform, basally truncate, with narrow, winged petioles; phyllaries 14-20 mm long at anthesis; ligules tightly involuted (appearing filiform) and enclosing the style. ..... *C. transiliens*
11. Leaves mostly elliptic, usually basally attenuate; phyllaries 8.5-13.0 mm long at anthesis; ligules not tightly (if at all) involuted. ..... (12)
   12. Phyllaries 1.8-2.8 mm wide with prominent, hyaline margins up to 0.5 mm wide; ligules purple beneath at maturity but without a midstripe; central (bisexual) flowers with fertile ovaries; achenes densely papillate; mature pappus bristles 10-13 mm long. ..... *C. hololeuca*
   12. Phyllaries 0.6-1.3 mm wide, the margins minutely stipitate-glandular, not hyaline; ligules with a purple, longitudinal midstripe beneath at maturity; central (bisexual) flowers with sterile ovaries; achenes sparsely papillate; mature pappus bristles 5.5-9.0 mm long. ..... *C. madrensis*

1. *CHAPTALIA TOMENTOSA* Vent. (Map 1, Figure 1).

Chaptalia tomentosa Vent., *Descript. Pl. Nouv. Jard. Cels*, fasc. 7, plate 61. 1802. *Gerbera walteri* Sch.-Bip. *in* Seemann, *nom. nov., Bot. Voy. Herald* 313. 1856. (non *Gerbera tomentosa* DC. 1838.). TYPE (as cited by Ventenat): "Plante herbacee, vivace, tres-commune aux environs de Charles-Town et dans les grands bois de la Caroline, cultivee chez Cels, de graines rapportees par Bosc." A specimen labeled "*Perdicium semiflosculare* Walter, Carol. Bosc" in the de Candolle herbarium is perhaps the collection originally studied by Ventenat (G-DC microfiche 1238, frame 15!).

Tussilago integrifolia Michx., *Fl. Bor.-Amer.* 2:121. 1803. *Chaptalia integrifolia* (Michx.) Nutt., *Gen. N. Amer. Pl.* 2:182. 1818. TYPE: "Amerique Septentrionale," with no other collection data, collector, or number. A

specimen of *Chaptalia tomentosa* in the Michaux herbarium (microfiche 99!) perhaps represents authentic material, but it bears no information except an annotation as "*Chaptalia*!", apparently by Asa Gray.

Thomas Walter (*Fl. Carolin.* 203-204. 1788.) identified a North American plant at his attention as *Perdicium semiflosculare* L. 1763 (an Old World species of *Gerbera*), apparently misapplying the earlier Linnaean name. Walter did not cite a specimen and gave his tentative identification simply as "*P. semiflosculare*?". Both Ventenat (1802) and Michaux (1803) referred to the identity of their proposed taxa (see above) with the plant referred to by Walter as *Perdicium semiflosculare*, but in the interpretation here, Ventenat and Michaux intended their names as the first valid description of this species, in contrast to Walter's nomenclatural misapplication. Study in the herbaria of Walter (BM), Michaux (or Richard, in P), and Ventenat (G-Delessert) ultimately may enable a more definitive discussion of these aspects of typification.

In contrast to the present interpretation, O. Kuntze and B.L. Robinson credited Walter with the legitimate authorship of the name *Perdicium semiflosculare* and proposed new combinations in *Thyrsanthema* and *Chaptalia*, respectively, based on the former. Technically, both of these later names may be interpreted as *nomina nuda* rather than new combinations, since *Perdicium semiflosculare*, if attributed to Walter, is without a type: *Thyrsanthema semifloscularis* Kuntze, *Rev. Gen. Pl.* 1:369. 1891.; *Chaptalia semifloscularis* B.L. Rob., Proc. Amer. Acad. Arts 45:412. 1910.

Plants produced singly; scapes ebracteate, elongating up to 40 cm in fruit. Leaves elliptic to elliptic-obovate, 5-18(-24) cm long, epetiolate, densely gray-white to tawny or orangish tomentose beneath, glabrescent above. Phyllaries 1.1-2.1 mm wide, eglandular. Ligules creamy-white with a purple midstripe beneath, 0.9-1.5 mm wide, the style 4.2-7.0 mm long with narrow branches 0.5-0.8 mm long. Bisexual flowers with sterile ovaries. Fertile achenes 3.5-5.2 mm long with a slender neck 1/4-1/5 as long as the achene, the body glabrous, sparsely pubescent in the neck region with extremely minute papillae. Chromosome number, $2n=48$ (Jones 1966).

Atlantic and Gulf coastal plain of the United States, from North Carolina to Florida and west through Alabama to eastern Texas, reported to be in the West Indies (Simpson 1978) but this based on the incorrect assumption that *Chaptalia azuensis* Urban & Eckman is a synonym of *C. tomentosa*; sandy soil in grass-sedge bogs (savannas) with scattered pines, usually in open areas but sometimes in thin woods, also commonly along edges of ditches; flowering December-April (-May in North Carolina).

Representative collections examined: UNITED STATES. Alabama: *Iltis 21538* (WIS). Florida: *Curtis 4507* (MSC,US). Georgia: *Nesom & Treiber s.n.* (NCU). Louisiana: *Allen 1805* (LSU). Mississippi: *Sargent* (WIS). North Carolina: *Nesom s.n.* (NCU). South Carolina: *Weatherby & Griscom 16654* (US). Texas: *Cory 52758* (DS,MICH,NY,SMU,US).

2. ***CHAPTALIA MADRENSIS*** Nesom, *spec. nov.* (Map 1, Figure 2). TYPE: MEXICO. Nuevo León: NW slope of Cerro Peña Nevada on road to western road crest (Puerto Pinos), ca. 1.5 km directly NW of summit, ca. 35 km ENE of Dr. Arroyo; steep slope, oak-pine-juniper with *Agave*, plants abundant in rocky, open areas and in shade of woods, ca. 2400 m, 31 Jul 1983, *G. Nesom 4758A*

(HOLOTYPE: US; Isotypes: CAS,ENCB,F,GH,K,MEXU,MICH,MO,MSC, NY,TEX,UC).

Chaptaliae tomentosae Vent. sect. *Chaptaliae* proxima corollis pistillatis ligulatis labium interior carentibus et achaeniis anguste rostratis sed differt praecipue foliis brevipetiolatis phyllariis glandulati-marginatis et acheniis longioribus papillatisque.

Plants produced singly; scapes ebracteate. Leaves elliptic to elliptic-obovate, 4-20(-32) cm long, with narrowly attenuate petioles, densely gray-white to tawny-white villous above and beneath. Phyllaries 0.6-1.3 mm wide, with conspicuously, minutely stipitate-glandular margins. Ligules creamy-white with a purple midstripe beneath, 1-2 mm wide, the style 6.3-8.8 mm long with narrow branches 0.9-1.7 mm long. Bisexual flowers with sterile ovaries. Fertile achenes 6-9 mm long with a slender neck 1/3-1/2 as long as the achene, the whole surface sparsely pubescent with short trichomes with rounded apices.

Nuevo León, Tamaulipas, San Luis Potosí, Querétaro, Hidalgo; pine, pine-oak-juniper, or evergreen oak, pine woods, sometimes at transition to matorral, apparently restricted to limestone, 1050-2500 m; flowering (January-)March-July.

Collections examined: MEXICO. Hidalgo: *Manning & Manning 53607* (GH, MEXU); *Mayfield 830* (MEXU,TEX); *Moore & Wood 3921* (GH,MICH); *Nesom 4372* (CAS,ENCB,F,MEXU,NY,TEX,UC,US) and *4373* (TEX); *Roe et al. s.n.* (WIS). Nuevo León: *Hinton 18250* (TEX), *18795* (TEX), *18958* (TEX), *20139* (TEX), *20140* (TEX), *22658* (TEX), *22750* (TEX), and *22819* (TEX); *Mueller & Mueller 274* (F,GH,MICH,TEX); *Nesom R575* (LL) and *R581* (LL); *Patterson 5912* (TEX). Querétaro: *Diaz Luna 19853* (TEX). San Luis Potosí: *Fryxell & Magill 2332* (ENCB); *McVaugh 12284* (MICH); *Nesom 4360* (TEX); *Palmer 222* (CM,F, MO,NY,US); *Rzedowski 5850* (ENCB), *6038* (ENCB,MICH), and *8738* (ENCB). Tamaulipas: *González Q. 3870* (ENCB); *Martínez 229* (TEX) and *1731* (TEX); *von Rozynski 692* (F,MICH,NY); *Runyon 842* (TEX,US); *Stanford et al. 731* (DS,NY) and *2407* (MICH,NY,SMU,TEX,UC,US-2 sheets).

Chaptalia madrensis is a common species of the eastern Sierra Madre, very often encountered in oak and pine-oak woods, where sterile individuals usually far outnumber the reproductive ones (pers. observ.). It often resembles *C. texana*, which differs in its central flowers with fertile ovaries, achenes with a thinner and longer neck, and narrower ligules lacking a purple midstripe.

3. *CHAPTALIA LYRATIFOLIA* Burkart (Map 2, Figure 3).

Chaptalia lyratifolia Burkart, Darwiniana 6:527. 1944. TYPE: MEXICO. Nuevo León: Sierra Madre above Monterrey, limestone ledges, 750 m (2500 ft), 29 Mar 1906, *C.G. Pringle 10207* (HOLOTYPE: SI; Isotypes: F!,GH!,GOET,MEXU-2 sheets!, MO!,MSC!,NY!,PH,UC!,US-2 sheets!, Z).

Strongly colonial, producing densely villous, scale-leaved rhizomes; scapes ebracteate, 4-20 cm tall. Leaves coriaceous, the base cordate or rounded, often lyrate with 1-4 pairs of deep lobes below the larger terminal one, the margins serrate or sinuate-serrate with slightly retrorse teeth, revolute. Heads 8-15 mm wide (pressed). Ligules creamy-white with a purple midstripe beneath. Bisexual flowers with sterile ovaries. Fertile achenes 3-4 mm long, unbeaked, pubescent over the whole surface with inflated, apiculate trichomes.

Coahuila, Nuevo León, Tamaulipas, San Luis Potosí; slopes over limestone, commonly with evergreen oaks, (750-)2100-2500 m; flowering (February-)March-August.

Collections examined: MEXICO. Coahuila: *Hinton 16706* (US), *20227* (TEX), *21074* (TEX); *Lyonnet 3490* (MEXU,US); *Palmer 544* (US). Nuevo León: *Hinton 18955* (TEX), *20195* (TEX), *22737* (TEX), *23953* (TEX); *Mayfield 1299* (TEX); *Nesom 4749* (ENCB,MEXU,TEX,US); *Pringle 2890* (GH). San Luis Potosí: *Palmer 222* (CM). Tamaulipas: *Dorr 2355* (TEX); *González Q. 3868* (ENCB); *Martínez 1732* (TEX); *Medrano et al. 8794* (MEXU) and *8835* (MEXU); *Nesom 1019* (ENCB,TEX), *1022* (TEX), *5981* (TEX); *Stanford et al. 731* (ARIZ,DS,GH,MO, NY).

Chaptalia lyratifolia is strongly colonial by thin rhizomes, but most collections have not included roots or rhizomes. Rhizome growth and plantlet production apparently peak before flowering, after which the rhizomes begin to degenerate.

4. ***CHAPTALIA ESTRIBENSIS*** Nesom, *spec. nov.* (Map 2, Figure 4). TYPE: MEXICO. Hidalgo: Mpio. Tenango de Doria, 8-11 km SW of Tenango de Doria, steep slope with *Quercus*; plants on cliff face, 1830-2140 m, 30 Oct 1983. *D.E. Breedlove 59571* with F. Almeda (HOLOTYPE: CAS!; Isotypes: ENCB!, MEXU!,MO!).

Chaptaliae lyratifoliae Burkart arcte affinis, a qua differt pubescentia fulvo-aurantiaca foliis ovatis nunquam lyratis phyllariis glandulati-marginatis ramis brevioribus stylorum bisexualium et acheniis longioribus.

Strongly colonial through rhizomes; scapes ebracteate. Leaves coriaceous, densely orange-tawny villous beneath, glabrescent above, the blades ovate to elliptic, with a cordate base with a sharply delimited petiole as long or longer than the blade, 20-75 mm wide, the margins coarsely serrate-apiculate, narrowly revolute. Heads 14-18 mm wide (pressed); phyllaries 10-13 mm long. Pistillate ligulate flowers 24-28 in 1(-2) series, the ligules white with a purple midstripe beneath. Bisexual flowers with sterile ovaries. Fertile achenes (2.0-)4.0-4.5 mm long, unbeaked, pubescent over the whole surface with inflated, apiculate to blunt-tipped trichomes.

Hidalgo and Veracruz, from there apparently disjunct to Cerro Azul in central Oaxaca; steep, moist banks and bases of boulders and cliffs, broad-leaved forests, sometimes with oaks and pines, 1750-2200 m; flowering February-April, October.

Collections examined: MEXICO. Hidalgo: 18 km E de Metepec hacia Tenango de Doria, 2200 m, 24 Mar 1980, *Hernández M. & Hernández V. 4124* (ENCB, MEXU-2 sheets); El Estribo, Tulancingo-Tenango de Doria highway, 9 Feb 1969, *Gimate Leyva s.n.* (ENCB); El Estribo, 21 Mar 1972, *Gimate Leyva 538* (ENCB); area of El Estribo, 20.8 km NE of Metepec, 10 Aug 1981 [past flower and fruit], *Nesom 4390* (ENCB,MEXU,MO,TEX,US); *Sharp 46195* (CAS,NY). Oaxaca: Cerro Azul (cima), near Río Grande, N of Niltepec, 2100 m, 7 Mar 1956, *T. McDougall s.n.* (CAS,MEXU). Veracruz: Mpio. Huayacocotla, road to Rancho Nuevo, Huayacocotla, 11 Feb 1972, *Hernández M. 1502* (TEX).

The northern collections of this species have been made from a small area in Hidalgo and adjacent Veracruz. The plants from the disjunct populations in Oaxaca differ slightly from the northern ones: the outer pistillate corollas are slightly smaller (9.5-12.5 mm long with ligules 0.8-1.3 mm wide vs. 12.5-19.0 mm long with ligules

1.3-2.0 mm wide) and the achenes are slightly shorter (2.0-2.5 mm long vs. 4.0-4.5 mm long). Otherwise, they are so similar that they must be considered conspecific.

5. *CHAPTALIA HINTONII* Bullock (Map 2, Figure 5).

Chaptalia hintonii Bullock, Hooker's Icon. Pl. 34:tab. 3346. 1937. TYPE: MEXICO. Edo. México: Dist. Temascaltepec, Nanchititla, cliffs, shade, 1 May 1933, *G.B. Hinton 3098* (HOLOTYPE: K; Isotypes: F!,GH!,MO!,TEX!,US!).

Colonial through thin rhizomes; scapes ebracteate. Leaves thin-herbaceous, often reddish, the margins widely crenate to shallowly lobed, dentate or serrate on the crenations or lobes, sometimes with lyratiform extensions of the blade below the cordate base. Scapes 10-37(-45) cm tall, ebracteate or with 1-3 linear bracts near the head. Heads 10-20 mm wide. Ligules whitish with a purple midstripe beneath. Bisexual flowers with sterile ovaries. Fertile achenes 4.0-4.8 mm long, not beaked, pubescent over whole surface with inflated, apiculate trichomes.

Edo. México, Guerrero; steep, moist slopes, often over rocks near water, oak or pine woods, 1700-2200 m; flowering March-May, August-November.

Collections examined: MEXICO. Locality not specified, probably 1792-1793 (see McVaugh 1977), *Sessé et al. 2670* (F, identified by the herbarium name "*Hieracium pusillum*"). Edo. México: *Hinton 3465* (ENCB,GH,MO,NY-2 sheets, OS,US-2 sheets); *Hinton 8562* (ARIZ-2 sheets, ENCB,F,GH,MEXU-2 sheets, MICH,MO,NY-3 sheets, TEX-2 sheets, US); *Matuda 30612* (MEXU-2 sheets). Guerrero: *Nesom 4409* (CAS,ENCB,F,GH,MEXU,MICH,MO,MSC,NY,TEX, UC,US); *Rzedowski 25225* (DS,ENCB,F,LL-2 sheets, MEXU,MICH,NY,US, WIS); *Rzedowski 26306* (ENCB,MICH).

The strongly colonial habit of *Chaptalia hintonii* results from the production of relatively long rhizomes. Many collections of the species have not included conspicuously rhizomatous plants, but this probably is at least partly the due to the relatively fragile connections of the rhizomes, because they can be unearthed by careful digging. It also is possible, as in *C. lyratifolia*, that the rhizomes are first produced at a different season than that in which most collections have been made, the rhizomes degenerating afterwards. Rhizomes of *C. hintonii* are somewhat woodier and more deeply subterranean than those of *C. lyratifolia* and *C. estribensis*, and they appear to lack the well-developed scale leaves present on the latter two species.

6. *CHAPTALIA PRINGLEI* Greene (Map 2, Figure 6).

Chaptalia pringlei Greene, Leafl. Bot. Observ. 1:192. 1906. LECTOTYPE (designated here): MEXICO. Oaxaca: La Hoya cañon above Domingillo, oak woods, 1500 m (5000 ft), 2 Nov 1894, *C.G. Pringle 5796* (US!; Isolectotype: GH!).

Simpson (1978) listed this species as a synonym of *Chaptalia dentata* (L.) Cass. and cited the type as *Pringle 5776*. As inferred from Pringle's journal (Davis 1936), Domingillo was near the Tomellin railroad station in north-central Oaxaca. Both type sheets bear a mixture of two species; on each sheet, one plant represents *C. pringlei* while the other two are *C. texana*. Greene's extremely abbreviated type description refers in part to *C. texana*, and the collection originally was identified as *C. nutans*, but the lectotypification here obviates the necessity of providing a new name for this species.

Plants produced singly; scapes with (1-)2-7 linear-filiform bracts 8-20 mm long, rarely ebracteate. Leaves oblanceolate, 3-24 cm long, the margins sinuate, very often shallowly retrorsely serrate or minutely denticulate, rarely entire. Heads turbinate to turbinate-cylindric, 8-14 mm wide. Flowers dimorphic, lacking a zone of eligulate pistillate ones; pistillate flowers 10-22 in 1-2 series, the ligules 1.5-2.8 mm wide, white with a purple midstripe, inner lip variable in size and presence; bisexual flowers with sterile ovaries. Fertile achenes 3.8-5.1 mm long, with a short, slightly constricted neck, prominently pubescent in the neck with spreading-ascending, swollen and apiculate trichomes.

Oaxaca, Puebla; open slopes in xerophytic matorral, often in oak-dominated vegetation, usually over limestone, 1800-2350 m; flowering May-August (-November).

Collections examined: MEXICO. Oaxaca: *Hugo & Conzatti 1866* (F,LL, MEXU); *Cruz C. 2115* (ENCB); *Mendoza 1461* (TEX); *Nesom 4405* (CAS,ENCB, GH,K,MEXU,MICH,MO,NY,TEX,UC,US); *Rzedowski 34853* (ENCB,UC,US); *Tenorio 9276* (TEX) and *18354* (TEX). Puebla: *Medrano et al. F941* (MEXU); *Purpus 1173* (F,GH,MO,NY,UC), *3128* (GH,NY,UC,US), and *3129* (F,GH,MO, NY,UC,US); *Tenorio 7998* (TEX).

7. *CHAPTALIA NUTANS* (L.) Polak. (Map 4, Figure 7).

Chaptalia nutans (L.) Polak., Linnaea 41:582. 1877; *non* (L.) Hemsley (1881).

BASIONYM: *Tussilago nutans* L., *Syst. Nat.* (ed. 10) 2:1214. October, 1759. *Leria nutans* (L.) DC., Ann. Mus. Natl. Hist. Nat. 19:68. 1812. *Gerbera nutans* (L.) Sch.-Bip. *in* Seemann, *Bot. Voy. Herald* 313. 1856. *Thyrsanthema nutans* (L.) Kuntze, *Rev. Gen. Pl.* 1:369. 1891. TYPE: AMERICA. Linnaeus cited only an illustration of this species, without collection data, from Plumier, *Pl. Amer.*, fasc. 2, plate 41, fig. 1! (1756). *Tussilago nutans*, however, was published with a phrase-name different from that of the plant illustrated by Plumier. Further, in the Linnaean herbarium (LINN) are two sheets of *C. nutans* (cat. nos. 995.5 and 995.7, microfiche!): the first is a Patrick Browne specimen received by Linnaeus in 1758 and annotated by him (C.E. Jarvis pers. comm.). This specimen was cited (together with a Sloane collection) in a separate description of *T. nutans* (a thesis, *Pl. Jam. Pug.* 23, November, 1759), and this account was given as the basis of the name in *Sp. Pl.* (ed. 2) 2:1213. (1763). "This later evidence together with Linnaeus's new phrase-name makes it clear that the Browne material, received prior to the publication of the name, must be regarded as syntype material together with the Plumier plate" (*fide* C.E. Jarvis). The specimen is the more preferable choice for the lectotype. LECTOTYPE (designated here): *P. Browne s.n.* (LINN, cat. no. 995.5).

Tussilago lyrata Pers., *Syn. Pl.* 2:456. 1807. *Leria lyrata* (Pers.) Cass., *Dict. Sci. Nat.* 26:102. 1823. TYPE: AMERICA MERIDIONALI. Persoon cited only "*Tussilago nutans* L., *Plum. Spec.* 14 ic. 41. f.1?" and it is not clear that he was proposing a name based on a type different from that of *Tussilago nutans* L. I have followed Cassini in treating the name as legitimate. In making the transfer of this species to *Leria*, Cassini cited the following specimen: HISPANIOLA. Santo Domingo: *Poiteau s.n.*, from the herbarium of Desfontaines (herb. DC., microfiche 1238!).

Tussilago vaccina Vell., *Fl. Flum.* 344-345. 1825. LECTOTYPE (Simpson 1975): BRAZIL. *Fl. Flum. Icon.* 8:plate 143. 1835. Illustration without collection data.

Chaptalia diversifolia Greene, Leafl. Bot. Observ. 1:194. 1906. TYPE: GUATEMALA. Vicinity of Mazatenango, ca. 350 m, 20 Feb 1905, *W.R. Maxon & R. Hay 3504* (HOLOTYPE: US!).

Chaptalia subcordata Greene, Leafl. Bot. Observ. 1:195. 1906. TYPE: ST. CROIX. Big Fountain garden, 24 Jun 1896, *A.E. Ricksecker 447* (HOLOTYPE: US!).

Chaptalia erosa Greene, Leafl. Bot. Observ. 1:196. 1906. TYPE: COSTA RICA. San José, bords des chemins et fosses, 1135 m, Jun 1892, *A. Tonduz 4147* (HOLOTYPE: US!).

Chaptalia majuscula Greene, Leafl. Bot. Observ. 1:196. 1906. TYPE: BOLIVIA. Mapiri, 5000 ft, May 1886, *H.H. Rusby 1677* (HOLOTYPE: US!).

Scapes ebracteate, 12-31 cm tall at anthesis, elongating to 22-81 cm in fruit. Leaves ovate to obovate, thin-herbaceous, 7-40 cm long with a petiolar region 1/5-3/5 as long as the leaf, thinly gray-pubescent beneath, strongly glabrescent above. Phyllaries linear-lanceolate, the inner 12-17 mm long, elongating in fruit to 15-25 mm. Flowers trimorphic, all fertile; ligules creamy, maturing to crimson, 0.2-0.5 mm wide, essentially without an inner lip; style 8.5-12.0 mm long with filiform branches (0.7)0.8-1.3(-1.5) mm long. Achenes sparsely papillate, 12-17 mm long, with a filiform neck 2-3 times as long as the body. Chromosome number, n=24 pairs (Baldwin & Speese 1947).

Tamaulipas, San Luis Potosí, Veracruz, Michoacán, Guerrero, Edo. México, Oaxaca, Tabasco, Chiapas, Yucatán?, Guatemala to Panamá and South America; usually in tropical or subtropical vegetation, often with evergreen oaks, less commonly with pines, 15-1500(-2200) m; flowering all year but most abundantly June-August.

Representative collections examined: BELIZE: *Lundell 6149* (F,MICH,NY,US).

COSTA RICA: *Skutch 2724* (LL,MICH,NY,US).

EL SALVADOR: *Standley 21535* (NY,US).

GUATEMALA: *Aguilar 118* (LL,MEXU,MICH).

HONDURAS. *Yuncker et al. 5639* (MICH,NY,US).

MEXICO. Chiapas: *Breedlove 39993* (DS,MEXU,MO). Dist. Federal: *Bravo s.n.* (MEXU). Guerrero: *Kruse 1184* (ENCB). Edo. México: *Hinton 1179* (MEXU, MO,NY,US-2 sheets). Michoacán: *Hinton 13919* (F,MO,NY). Oaxaca: *Martínez C. 1377* (ENCB,MEXU); *Poole 1265* (LL). Puebla: *Sharp & Miranda 3438* (MEXU). San Luis Potosí: *Edwards 635* (F,TEX); *Roe & Roe 2311* (ENCB,LL, WIS). Tabasco: *Conrad 2801* (MO); *Rovirosa 138* (MEXU-2 sheets). Tamaulipas: *Sullivan 618* (DUKE,NY,TEX); *Patterson 7327* (TEX). Veracruz: *Dressler & Jones 178* (MEXU,MICH,US); *Ventura 8104* (ENCB,MEXU,MICH,NY).

NICARAGUA: *Seymour 2780* (F,NY,UC).

PANAMA: *Cooper 267* (F,MICH,NY,US).

8. *CHAPTALIA TEXANA* Greene (Map 4, Figure 8).

Chaptalia texana Greene, Leafl. Bot. Observ. 1:191. 1906. *Chaptalia nutans* (L.) Polak. var. *texana* (Greene) Burkart, Darwiniana 6:569. 1944. TYPE: UNITED STATES. Texas: "rocky, sparsely wooded ground in western Texas," Oct 1890, *G.C. Neally 297* (HOLOTYPE: US!).

Chaptalia carduacea Greene, Leafl. Bot. Observ. 1:191. 1906. TYPE: UNITED STATES. Texas: Duval Co., San Diego, 1885, *M.B. Croft 35* (HOLOTYPE: US!; Isotype: MICH!).

Chaptalia leonina Greene, Leafl. Bot. Observ. 1:193. 1906. TYPE: MEXICO. Nuevo León: Monterrey, 17-26 Feb 1880, *E. Palmer 764* (HOLOTYPE: US!; Isotypes: NY!,US!).

Chaptalia petrophila Greene, Leafl. Bot. Observ. 1:193. 1906. TYPE: MEXICO. Jalisco: rocky hills near Guadalajara, 5000 ft, 22 Jul 1902, *C.G. Pringle 11315* (HOLOTYPE: US!; Isotypes: F!,GH!,SI). According to Pringle's journal (Davis 1936), the type collection probably was made in "the barranca below the waterfall of Rio Blanco." This locality apparently was near the "Oblatos R.R.," northwest of Guadalajara, west of Zapopan. See further comments below.

Scapes ebracteate, 13-34 cm tall at anthesis, elongating to 16-46 cm in fruit. Leaves obovate to ovate or elliptic, relatively thick, 2.5-21.0 cm long with a petiolar region 1/8-1/3 as long as the leaf, the blade 12-35(-55) mm wide, densely gray-white pubescent beneath, glabrescent above but usually remaining sparsely pubescent until after flowering. Phyllaries linear-lanceolate, the inner 14-16(-18) mm long, not elongating in fruit. Flowers trimorphic or dimorphic (see comments below), all fertile; ligules creamy, maturing to crimson, 0.2-0.8 mm wide, essentially without an inner lip; pistillate style 8.8-12.0 mm long with filiform branches (0.7)0.8-1.3(-1.5) mm long. Achenes sparsely to moderately papillate, 11.5-13.0 mm long, with a filiform neck 1.0-1.6 times as long as the body. Chromosome number, n=24 pairs (Turner 1959).

United States in south-central and southwestern Texas and probably extreme south-central New Mexico (see citation of *Parry et al. 674* below), México in Baja California Sur, Chihuahua, Coahuila, Nuevo León, Tamaulipas, San Luis Potosí, Nayarit, Jalisco (*Chaptalia petrophila*), Guanajuato, Querétaro, Hidalgo, Edo. México, Puebla, and Oaxaca; slopes in thin, rocky soil, most often in oak woods, (250-)1300-2550 m; flowering March-June in Texas (excluding Brewster Co.), all year elsewhere but most abundantly August-October. A collection from northern Aguascalientes (*Rzedowski 24988*) identified by McVaugh (1984) as *C. nutans* var. *texana* is instead *C. hololeuca*.

Representative collections examined: UNITED STATES. New Mexico: Mexican boundary survey, chiefly in the Valley of the Rio Grande, below Doñana, *Parry et al. 674* (US-2 sheets). Texas: *Tracy 8959* (MO,MSC,NY,US,WIS).

MEXICO. Baja California Sur: Sierra de las Palmas, La Campagne, S of Santa Rosalia, 27-29 Apr 1952, *Gentry & Fox 11768* (DUKE,MEXU-2 sheets, MICH). Chihuahua: Sta. Eulalia plains, 1885, *Wilkinson s.n.* (MU); Sierra del Roque N of Julimes, 24 Aug 1973, *Johnston et al. 12332a* (LL); Mpio. Temosachi, Nabogame, 27 Oct 1988, *Laferrière 2201* (ARIZ,TEX). Coahuila: *Wendt & Riskind 1659* (LL). Guanajuato: *McVaugh 24175* (DUKE,ENCB,LL,MICH,NY,US). Hidalgo: *González Q. 3155* (ENCB,MICH). Edo. México: *Rzedowski 20902* (ENCB, MICH,MSC). Nuevo León: *Pringle 10169* (ARIZ-2 sheets, ASU,CAS,COLO,F, MEXU-3 sheets, MICH,MO,MSC,NMC,NY,OKLA,SMU,TEX,UC,US). Oaxaca: *Stevens 1208* (DUKE,ENCB,MICH,MO,MSC,OS). Puebla: *Purpus 3127* (F,GH, MO,NY,UC,US). Querétaro: *Arguelles 844* (MEXU). San Luis Potosí: *Rzedowski 10233* (ENCB). Tamaulipas: *Palmer 527* (F,NY,US).

Some heads of *Chaptalia texana* completely lack ligulate pistillate flowers, but this does not appear to be correlated with geography or season and is sometimes variable within populations, where ligulate and eligulate heads are both produced (e.g., *Pringle 10169* - Nuevo León, Apr; *Pringle 11315* - Jalisco [*C. petrophila*], Jul; *Rzedowski 20902* - Edo. México, Oct; *Croft 35* - Texas, without specific date).

Chaptalia texana has been considered conspecific with *C. nutans*, but the former has smaller, thicker, and fewer-lobed leaves with more silvery-white pubescence on the heads and lower leaf surfaces, more persistently pubescent, longer style branches, and other differences as in the key. They also are separated ecologically, with *C. texana* occurring in inland, relatively arid habitats and *C. nutans* typically in tropical ones.

The longest pistillate style branches in *Chaptalia texana* occur in plants from Querétaro and México (2.0-2.3 mm) and the shortest occur in plants from Puebla and Oaxaca (1.0-1.6 mm), where the style branch length overlaps with that of *C. nutans*. Even though the two taxa are clearly differentiated over most of their ranges, apparent intermediates occur in Edo. México, Puebla, and Oaxaca, where their geographic ranges appear to interdigitate.

The six plants of *Chaptalia texana* studied from Baja California Sur (*Gentry & Fox 11768*) are slightly differentiated from those in the rest of the range: the heads range wider (to 20 mm pressed vs. 11-17 mm) and the phyllaries average slightly longer. The outer pistillate flowers are bilabiate with an inner lip 0.5-2.0 mm long, and abortive stamens ("staminodes") were found in several inner pistillate flowers from the head of one plant. These latter structures were not observed in any other plants of *C. texana*. The differences appear to be minor, and long geographic disjunctions occur within other species of the genus, although *C. texana* seems to be the most peripherally scattered. *Chaptalia* was not included among the genera of Baja California in the recent treatment by Wiggins (1980), but these plants appear to be native elements of the flora.

The identity of *Chaptalia petrophila* is somewhat problematic. In its ebracteate scapes, phyllary morphology, and papillate achene vestiture, it is very similar to *C. texana* and *C. nutans*. The pistillate style branch length of 1.3-1.8 mm and the complete lack of ligulate pistillate flowers suggest that it is best placed with *C. texana*, but the broadly obovate-oblanceolate leaves with merely mucronulate margins are anomalous in that species. Further, the type collection (from near Guadalajara, Jalisco) is geographically out of range for both *C. texana* and *C. nutans* (Map 4). Like the plants from Baja California Sur, however, I am treating *C. petrophila* as a peripheral variant of *C. texana*. See further comments below regarding *C. spathulata*.

9. *CHAPTALIA TRANSILIENS* Nesom (Map 3, Figure 9).

Chaptalia transiliens Nesom, Rhodora 86:127. 1984. TYPE: MEXICO. Nuevo León: NW slope of Cerro Peña Nevada on road to western pass (Puerto Pinos), ca. 1.5 km NW of the summit, ca. 35 km ENE of Dr. Arroyo; steep slope, oak-pine-juniper with *Agave*, 31 Jul 1983, *G. Nesom 4759* (HOLOTYPE: US; Isotypes: ANSM,CAS,ENCB,F,GH,K,MEXU,MICH,MO,NY,OS,SMU,TEX, UC).

Scapes ebracteate or with a linear bract within 5 mm of the head. Leaves thick, spatulate (panduriform), the blades 6-28 cm long, elliptic to ovate-elliptic, sometimes sublyrate with several shallow lobes at the base, with narrow, winged petioles, densely tawny-gray pubescent beneath, quickly glabrescent above. Phyllaries 14-20 mm long at anthesis (not elongating further), the outer with stipitate-glandular margins, the inner with wide, flange-like, scarious margins. Ligules erect, 11-17 mm long, involuted (appearing filiform) and enclosing the style branches, white above and reddish-purple beneath at early anthesis, completely dark purple at maturity. Achenes

7-11 mm long, with a narrow beak about as long as the body, pubescent over the whole surface with prominently attenuate-apiculate papillae.

Coahuila, Nuevo León, Tamaulipas, San Luis Potosí, Guanajuato, Hidalgo, Edo. México, Puebla, Oaxaca, disjunct to Chiapas and Guatemala; steep, moist, shaded slopes, usually with pine, oak, pine-oak, or oak-pine-juniper, less commonly in drier habitats with thorny shrubs, 1600-2550 m; flowering (January-)April-October (-November).

Collections examined: GUATEMALA. *Johnston 1765* (F); *Standley 81939* (F); *Steyermark 50351* (F).

MEXICO. Chiapas: *Breedlove 6870* (DS) and *41026* (DS); *Breedlove & Almeda 47775* (CAS); *Laughlin 740* (DS,MICH); *Matuda 4686* (MEXU,MO,NY) and *18243* (MEXU). Coahuila: *Villarreal 5417* (TEX). Guanajuato: *Arguelles 1574* (MEXU); *McVaugh 24173* (NY). Hidalgo: *Nesom 4377* (MEXU,MICH,TEX,US). Edo. México: *Rzedowski 26002* (ENCB). Nuevo León: *Hinton 19685* (TEX), *20218* (TEX), *21328* (TEX), *21631* (TEX); *Meyer & Rogers 2575* (MO,US); *Mueller & Mueller 437* (GH,MICH,TEX,US); *Nesom 7119b* (TEX). Puebla: *Ventura 5719* (ENCB,MICH); *Beaman 3620* (MSC); *Nesom 4398* (CAS,ENCB,F,K,MEXU, MICH,NY,TEX,UC); *Purpus s.n.* (UC). San Luis Potosí: *Nesom 4361* (CAS, COLO, ENCB, K, MEXU, MICH, MSC, NY, TEX, US); *Prather 915* (TEX). Tamaulipas: *Nesom 7459* (TEX).

Chaptalia transiliens is distributed over a remarkably wide area and is amply distinct from other species, although it has been confused with *C. nutans* and *C. texana*. At the type locality, it was growing with *C. texana* and *C. madrensis*.

10. *CHAPTALIA HOLOLEUCA* Greene (Map 5, Figure 10).

Chaptalia hololeuca Greene, Leafl. Bot. Observ. 1:192. 1906. TYPE: MEXICO. Coahuila: Saltillo, in depression on slope of stony hillside, May 1898, *E. Palmer 192* (HOLOTYPE: US!; Isotype: GH!).

Scapes ebracteate. Scapes and leaves moderately to densely silver-white villous beneath, less densely so above and tardily glabrescent. Phyllaries in 2-3(-5) series, 1.8-2.8 mm wide, with broad and prominent hyaline margins. Heads few-flowered; style branches of the pistillate flowers somewhat flattened, barely extending out of the tube. Achenes 5.5-8.0 mm long, with a short beak, 6-9-ribbed, densely papillate.

Coahuila, Nuevo León, Tamaulipas, San Luis Potosí, Querétaro, Aguascalientes, Hidalgo; dry, open slopes, usually over limestone (gypsum in Nuevo León), matorral or chaparral, often with oaks, sometimes with scattered pines or pine-juniper, 1150-2300 m; flowering February-April, July-October.

Collections examined: MEXICO. Aguascalientes: *Rzedowski 24988* (ENCB, MICH). Coahuila: *Arsene 10223* (US); *Hinton 20228* (TEX); *Johnston & Mueller 417* (GH); *Jones 298* (MO,MSC,US); *Palmer 528* (GH,NY,US); *Purpus 1019* (F, GH,MO,NY,UC) and *1019a* (UC). Hidalgo: *Purpus s.n.* (UC). Nuevo León: *Hinton 19685* (TEX), *20114* (TEX), *20121* (TEX), *21788* (TEX), *23842* (TEX); *Nesom 7698* (TEX). San Luis Potosí: *Bustos Z. s.n.* (ENCB); *Henrickson 17590d* (TEX); *Lundell 5744* (MICH,US). Tamaulipas: *Henrickson 19140* (TEX); *Martínez 1044* (TEX).

Chaptalia hololeuca has sometimes been identified as *C. texana*, but the two are clearly distinct and the former is nearly completely restricted to the Chihuahuan Desert region. The most distinctive features of *C. hololeuca* are the following: relatively short stems and small leaves with upper surface usually remaining pubescent at flowering;

phyllaries in 2-3(-5) series, broad and often with prominent, hyaline flanges; flowers relatively few; pistillate style branches somewhat flattened, barely extending out of the tube; and achenes with a short beak, 6-9 ribbed, the whole surface densely papillate. *Jones 298* differs from other plants of the species in two respects: the achene beaks are slightly longer and one of the several mounted plants has a single small bract on the stem, well below the head.

11. *CHAPTALIA ALBICANS* (Sw.) Vent. *ex* Steudel (Map 5, Figure 11).

Leontodon tomentosum L. *f.*, *Suppl. Pl. Syst. Veg.* 347. 1781. [1782.]. *Tussilago albicans* Sw., *nom. nov.*, *Nov. Gen. Sp. Pl. Prodr.* 113. 1788 (not *Tussilago tomentosum* Ehrh. 1788.). *Leria albicans* (Sw.) DC., Ann. Mus. Natl. Hist. Nat. 19:68. 1812. *Chaptalia albicans* (Sw.) Vent. *ex* Steudel, *Nom. Bot.* (ed. 2) 1:344. 1840. (not *Chaptalia tomentosa* Vent. 1802.). *Gerbera albicans* (Sw.) Sch.-Bip. *in* Seemann, *Bot. Voy. Herald* 313. 1856. *Thyrsanthema tomentosa* (L. *f.*) Kuntze, *Rev. Gen. Pl.* 1:369. 1891. LECTOTYPE (Nesom 1984b): JAMAICA? *Patrick Browne s.n.* (LINN, no. 953.16, microfiche 537!).

Leria leiocarpa DC., *Prodr.* 7:42. 1838. *Gerbera leiocarpa* (DC.) Sch.-Bip. *in* Seemann, *Bot. Voy. Herald* 313. 1856. *Leria nutans* (L.) DC. var. *leiocarpa* (DC.) Griseb., *Cat. Pl. Cubens.* 158. 1866. *Chaptalia nutans* (L.) Polak. var. *leiocarpa* (DC.) A. Hitchc., Ann. Rep. Missouri Bot. Gard. 4:102. 1893. *Chaptalia leiocarpa* (DC.) Urban, *Symb. Antill.* 8:747. 1921. TYPE: CUBA. No other locality data, 1825, *Ramón de la Sagra s.n.* (HOLOTYPE: G-DC, microfiche 1239!). See Nesom 1984b.

Chaptalia obovata C. Wright *in* Sauvalle, Ann. Acad. Cien. Habana 6:212. 1870. TYPE: CUBA. En la loma Pelada, jurisdicción de los Palacios, *C. Wright 3617* (GH!,NY-2 sheets!, US!). See Nesom 1984b.

Chaptalia fallax Greene, Leafl. Bot. Observ. 1:195. 1906. TYPE: CUBA. Vicinity of Baracoa, 24-29 Jan 1902, *C.L. Pollard et al. 86* (HOLOTYPE: US!; Isotypes: NY!,US!).

Chaptalia crispula Greene, Leafl. Bot. Observ. 1:194. 1906. TYPE: GUATEMALA. Dept. Sta. Rosa: Sta. Rosa, 3000 ft, Jun 1892, *Heyde & Lux 3433* (HOLOTYPE: US!; Isotypes: F!,GH!,NY!,US!).

Scapes 6-15 cm tall at anthesis, 12-30(-37) cm at fruiting, ebracteate, prominently dilated immediately beneath the head. Leaves 1.7-14.0 cm long, epetiolate or attenuate to a short petiolar region, the margins retrorsely serrulate- to denticulate-apiculate. Heads always erect. Ligules 0.2-0.3 mm wide. Achenes 8.4-11.2 mm long, the filiform beak 1/2-2/3 as long as the achene, glabrous to sparsely glandular-pubescent, usually only along the ribs. Chromosome numbers, n=24, ca. 29 pairs (Torres & Liogier 1970).

San Luis Potosí, Veracruz, Yucatán, Chiapas, to Belize and Honduras, the West Indies, and southern Florida; grassy areas or open savannas, sometimes near evergreen oaks, (350-)1100-1835 m; flowering (March-)April-July(-November).

For comments and citations of collections examined, see Nesom (1984b).

12. *CHAPTALIA RUNCINATA* Kunth (Map 3, Figure 12).

Chaptalia runcinata Kunth, *Nov. Gen. Sp. Pl.* 4 [folio]:5, tab. 303. 1820. *Loxodon longipes* Cass., *nom. nov. illeg.*, *Dict. Sci. Nat.* 27:255. 1823. *Tussilago bicolor* Willd. *ex* Less. [*pro syn. sub Oxydon bicolor*], *nom. nov. illeg.*, Linnaea 5:357.

1830. *Oxydon bicolor* (Willd. *ex* Less.) Less., *nom. illeg.*, Linnaea 5:357. 1830. *Gerbera bicolor* (Willd. *ex* Less.) Sch.-Bip., *Bot. Voy. Herald* 313. 1856. *Thyrsanthema runcinata* (Kunth) Kuntze, *Rev. Gen. Pl.* 1:369. 1891. TYPE: COLOMBIA. "Crescit locis temperatis, scopulosis Andium Novo-Granatensium in ripa fluvii Smita, alt. 590 hex. Floret Octobri," *Humboldt & Bonpland 2031*. Two duplicates of the type collection are known: (1) P, herb. H.B.K. microfiche 89!, the specimen marked as number "2031," also see McVaugh (1972), and (2) herb. Willdenow, cat. no. 15714, microfiche! Neither specimen, however, matches the illustration in the original publication, which shows a single plant with three heads at anthesis. LECTOTYPE (designated here): P, the H.B.K. number 2031.

Scapes 8-15 cm tall at anthesis, to 28 cm at fruiting, with 5-8 lanceolate bracts. Leaves subcoriaceous, oblong-obovate to elliptic, 3-9 cm long, 5-15 mm wide, densely gray-white tomentose beneath, glabrous above, the margins narrowly revolute, with 4-8 shallowly serrate or dentate teeth. Heads turbinate-cylindric, 5-8 mm wide, with glabrous or glabrate phyllaries 11-16 mm long. Achenes (5.0-)6.5-7.8 mm long, beaked, basally papillate, otherwise glabrous, purple or brown at maturity.

Sonora, Sinaloa, Durango, Nayarit, apparently disjunct to Edo. México and Hidalgo, again disjunct to Costa Rica (as reported by Simpson 1975) and Panamá, more widespread at high altitudes in South America (Venezuela and Colombia southward along the Andes to Bolivia, Paraguay, southern Brazil, Uruguay, and Argentina); moist or wet meadows, often at the edge of the wettest part, areas of oak, pine, fir, or mixtures, (990-)2100-3100 m; flowering June-October (January in Hidalgo).

Collections examined: MEXICO. Dist. Federal: *Rzedowski 35360* (ENCB). Durango: *Breedlove 44171* (CAS,ENCB); *Cronquist 9560* (MICH,NY); *Detling 8437* (US); *Fryxell 3034* (ENCB,OS); *González & Rzedowski 2343* (TEX); *LeDoux & Dunn 1960* (ENCB, NY); *Maysilles 7809* (ENCB,MICH), *7848* (MICH-2 sheets) and *7452* (ENCB,MICH); *Mick & Roe 68* (ENCB,WIS-2 sheets); *Nesom 4432* (CAS,ENCB, F, GH, GUADA, MEXU, MICH, MO, NY, TEX, UC, US) and *4439* (ENCB,MEXU,MICH,TEX); *Parker 645* (LL); *Ripley & Barneby 13990* (NY); *Waterfall & Wallis 13583* (OKLA,SMU); *Worthington 8810* (TEX,UTEP). Hidalgo: *Rzedowski 32698* (ENCB). Edo. México: *Hinton 8478* (GH,US); *Poole 1567* (MEXU,TEX); *Rzedowski 36288* (ENCB). Nayarit: *Rose 2022* (GH,NY,US); *Breedlove 44497* (CAS). Sinaloa: *Pennell 20142* (US). Sonora: *Pennell 19647* (GH,MICH,NY,US).

PANAMA. *Stearn et al. 1189* (MO).

Burkart (1944) considered *Chaptalia runcinata* to have two varieties in South America, var. *runcinata* and var. *graminifolia* Dusen. More recently, Cabrera (in Cabrera & Klein 1973) elevated the latter to specific rank as *C. graminifolia* (Dusen) Cabrera.

Chaptalia runcinata from Argentina was reported by Burkart (1944) to produce chasmogamous and cleistogamous heads in seasonal alternation, as occurs in plants of the genus *Leibnitzia* (*e.g.*, see Nesom 1983). I have not observed this phenomenon among collections of *C. runcinata* made from México or Central America, all of which have been chasmogamous.

UNCERTAIN OR EXCLUDED TAXA

The status of *Chaptalia spathulata* (D. Don) Hemsl.

Chaptalia spathulata has ebracteate stems and strongly bicolored, elliptic, essentially entire leaves. It is similar to *C. nutans* and *C. texana*, but the leaves are more similar in shape to those of *C. petrophila* than to typical forms of either of the former, and the heads are atypically small for *C. nutans* or *C. texana*. Further, the type locality of *C. spathulata* is an area where neither *C. nutans* nor *C. texana* has been collected but where both might reasonably be expected (Map 4).

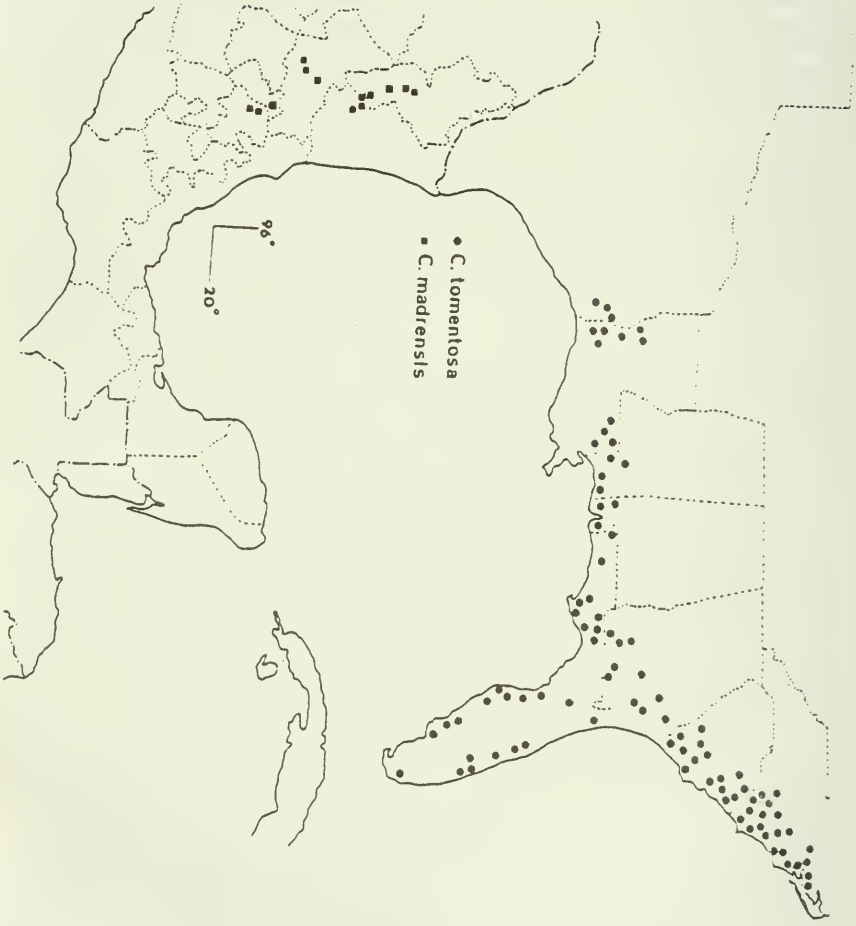
Don noted that the central flowers of *Chaptalia spathulata* were "masculine." I believe this may have been a mistaken conclusion based on observation of immature achenes, but if such proves to be true, *C. spathulata* would have to be interpreted as a rare species of sect. *Chaptalia*. A definite decision regarding disposition of *C. spathulata* must await an examination of the type specimens.

CHAPTALIA SPATHULATA (D. Don) Hemsl., Biol. Centr.-Amer., Bot. 2:255. 1881. BASIONYM: *Leria spathulata* D. Don, Trans. Linn. Soc. London 16:249. 1833. *Lieberkuhna spathulata* (D. Don) DC., *Prodr.* 7:43. 1838. *Gerbera spathulata* (D. Don) Sch.-Bip. *in* Seemann, *Bot. Voy. Herald* 313. 1856. *Thyrsanthema spathulata* (D. Don) Kuntze, *Rev. Gen. Pl.* 1:369. 1891. *Cacalia spathulata* Sessé & Moçiño *ex* D. Don [*pro syn. sub Leria spathulata* D. Don], Trans. Linn. Soc. London 16:249. 1833. *Cacalia spathulata* Sessé & Moçiño, *nom. illeg.* Naturaleza (México City) ser. 2, 1:132. 1890. PROBABLE TYPE: MEXICO. [Guerrero]: in the Mazatlán mountains, July [1797], *Sessé & Moçiño 2028* (MA, photo-F!). Other Sessé & Moçiño collections of this taxon are the following: *s.n.* (FI herb. Webb, marked by Pavón as "*Cacalia spathulata* N.E.," photo-US!); *3370* (MA, photo-F!); *4062* (MA, photo-F!). The collection locality (except for the state) and date were cited by Sessé & Moçiño in the publication of *Cacalia spathulata*. According to McVaugh (1977), the collection was made in the autumn of 1789 near what is now called Chilpancingo. McVaugh (pers. comm.) could not locate a specimen of this at Oxford [herb. OXF].

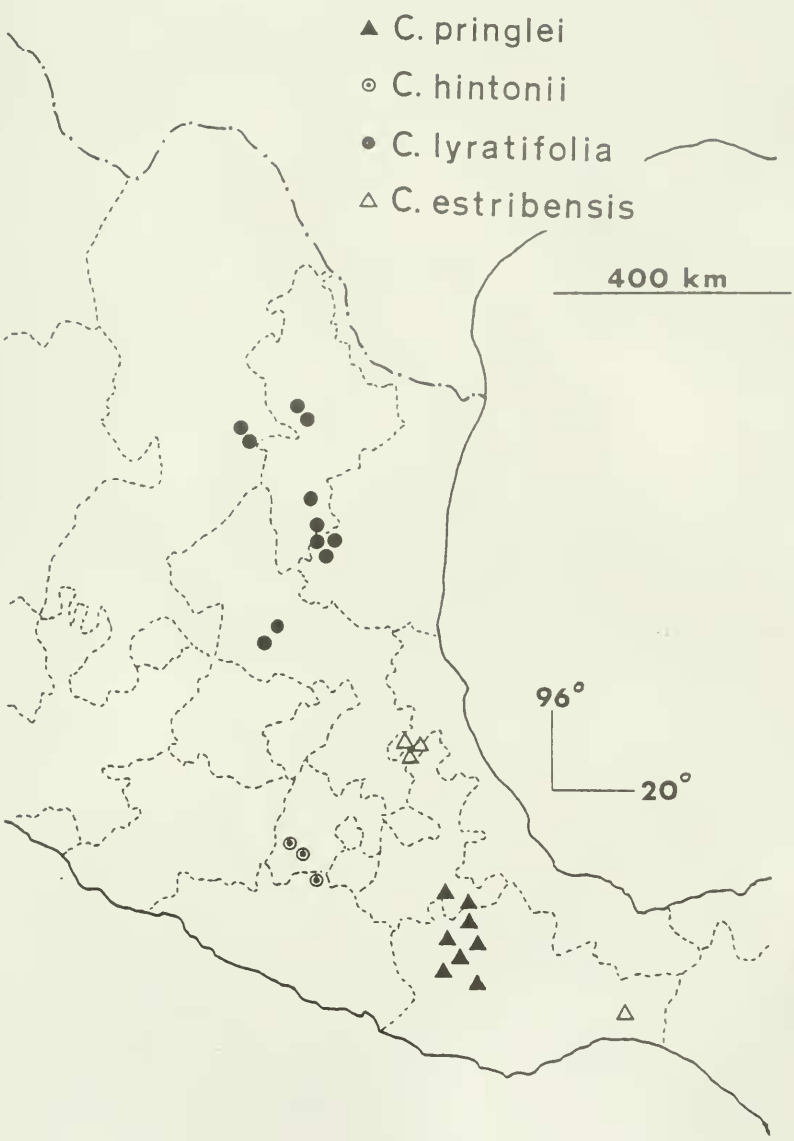
The status of *Chaptalia lyrata* D. Don

After locating the type specimens of *Chaptalia lyrata* D. Don at OXF and receiving photographs and detailed observations of micromorphology, it is clear that it is the earliest named taxon representing what I have previously identified as *Leibnitzia seemannii* (Sch.-Bip.) Nesom. For additional synonymy, see Nesom (1983).

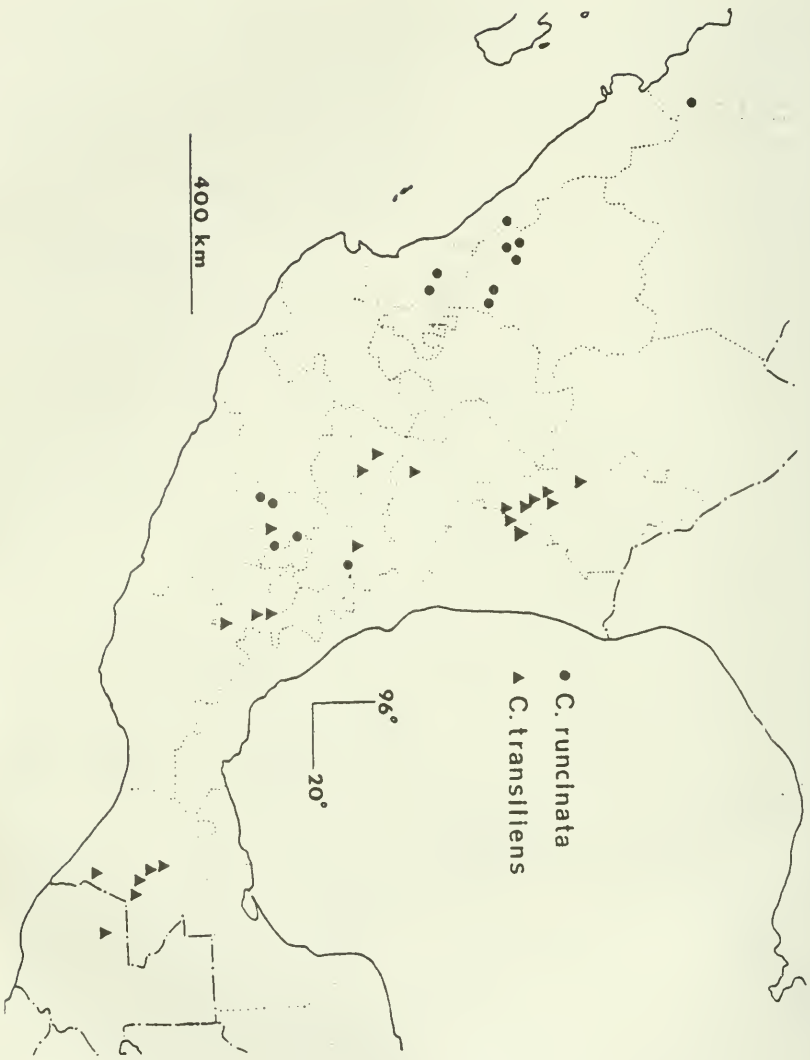
LEIBNITZIA LYRATA (D. Don) Nesom, *comb. nov.* BASIONYM: *Chaptalia lyrata* D. Don, Trans. Linn. Soc. London 16:243. 1833. *Gerbera lyrata* (D. Don) Sch.-Bip. *in* Seemann, *Bot. Voy. Herald* 313. 1856. *Thyrsanthema lyrata* (D. Don) Kuntze, *Rev. Gen. Pl.* 1:369. 1891. *Hieracium stipitatum* Sessé & Moçiño *ex* Don [*pro syn. sub Chaptalia lyrata* D. Don], Trans. Linn. Soc. London 16:243. 1833. Not *Leria lyrata* (Pers.) Cass. = *Chaptalia nutans* (L.) Polak.; not *Tussilago lyrata* Willd. (1803) = *Chaptalia lyrata* (Willd.) Spreng. (1826) = *Leibnitzia anandria* (L.) Turcz.; not *Perdicium lyratum* R. Br. *ex* Steud., *Nom. Bot.* (ed. 2) 2:203. 1841. (illegitimate combination or new name based simply on "*Chaptalia lyrata*"). TYPE: MEXICO. No other locality data or date, *Sessé & Moçiño s.n.*



Map 1. Distribution of *Chaptalia tomentosa* and *C. madrensis*.



Map 2. Distribution of *Chaptalia lyratifolia*, *C. estribensis*, *C. hintonii*, and *C. pringlei*.



Map 3. Distribution of *Chaptalia runcinata* and *C. transiliens*.

Map 4. Distribution of *Chaptalia nutans* and *C. texana*. The "S" shows the locality of *C. spathulata* (see comments in text).

Map 5. Distribution of *Chaptalia hololeuca* and *C. albicans*.

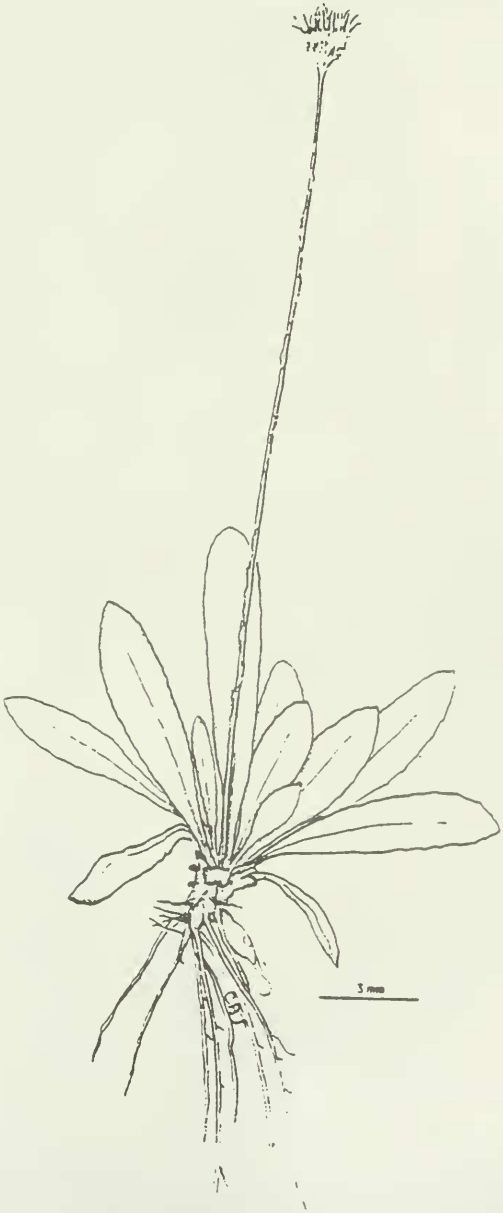


Figure 1. Habit of *Chaptalia tomentosa* (*Iltis 25151*).

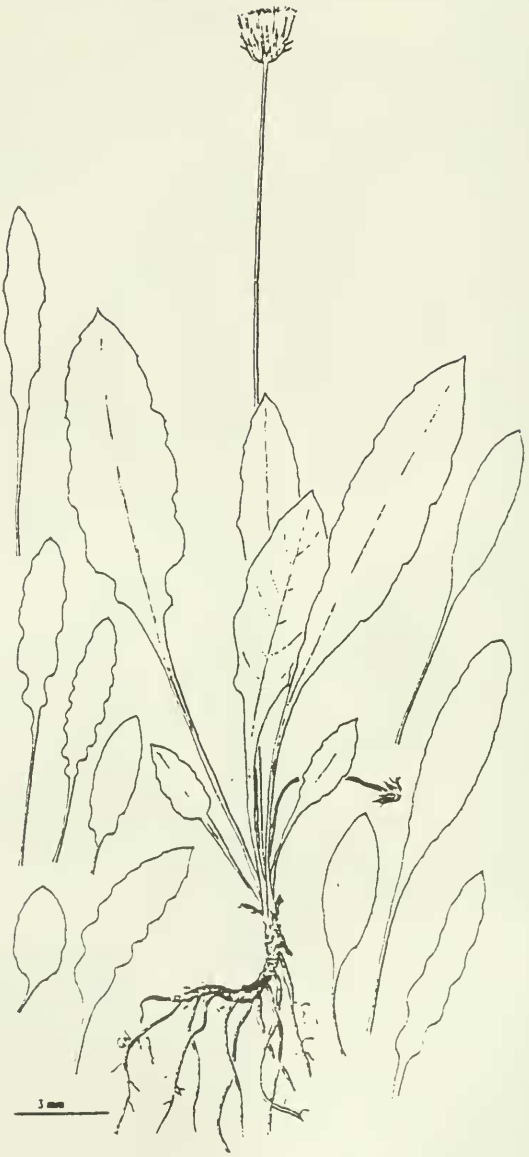


Figure 2. Habit and leaf variation of *Chaptalia madrensis* (*Nesom 4758*). Disconnected leaves show species variability at × 2/3 scale of full plant.

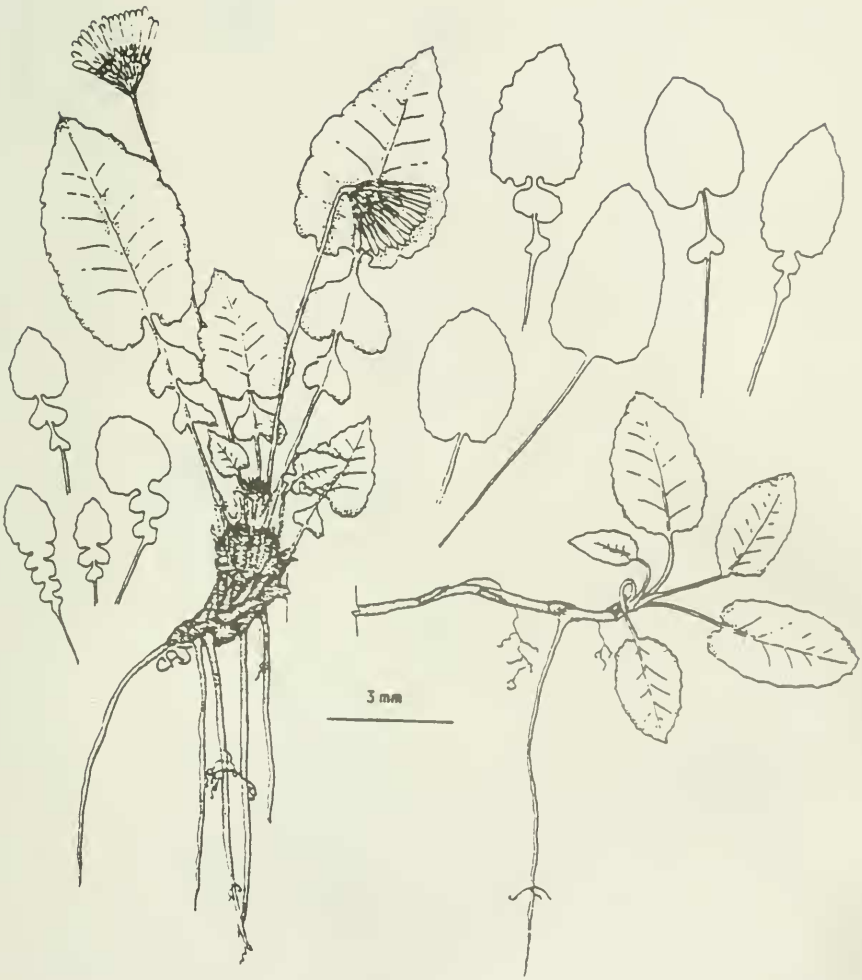


Figure 3. Habit of *Chaptalia lyratifolia* (*Lyonnet 3490* with stoloniferous branch of *Nesom 1019*). Disconnected leaves show species variability at × 2/3 scale of full plant.

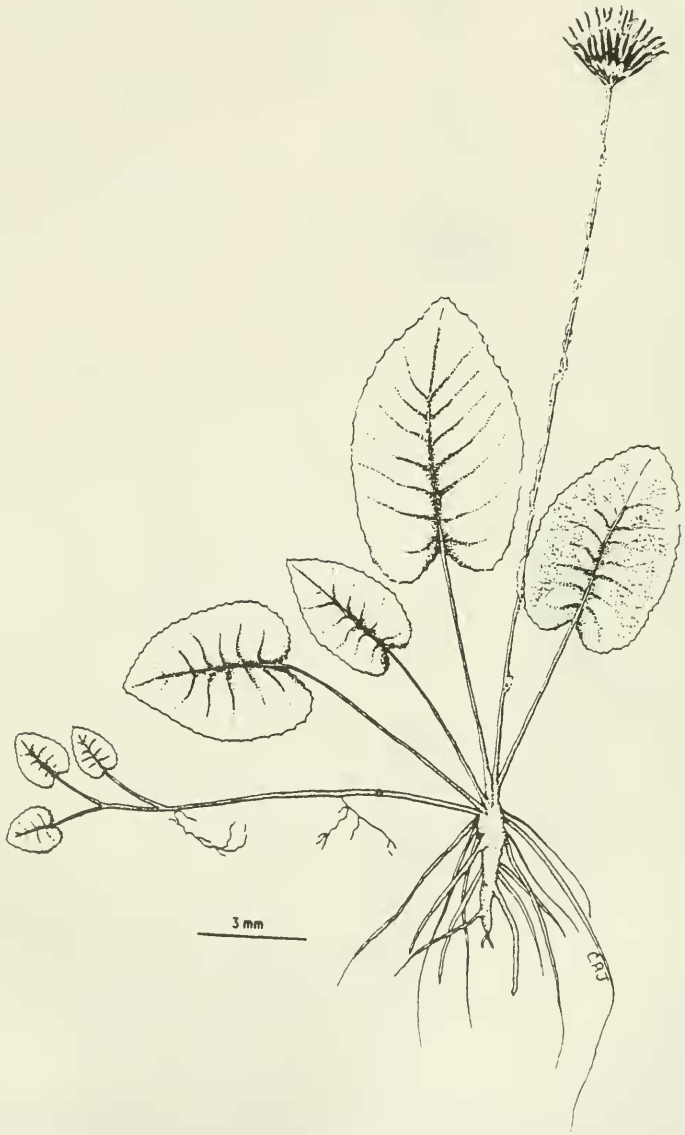


Figure 4. Habit and leaf variation of *Chaptalia estribensis* (*Gimate L. s.n.*).

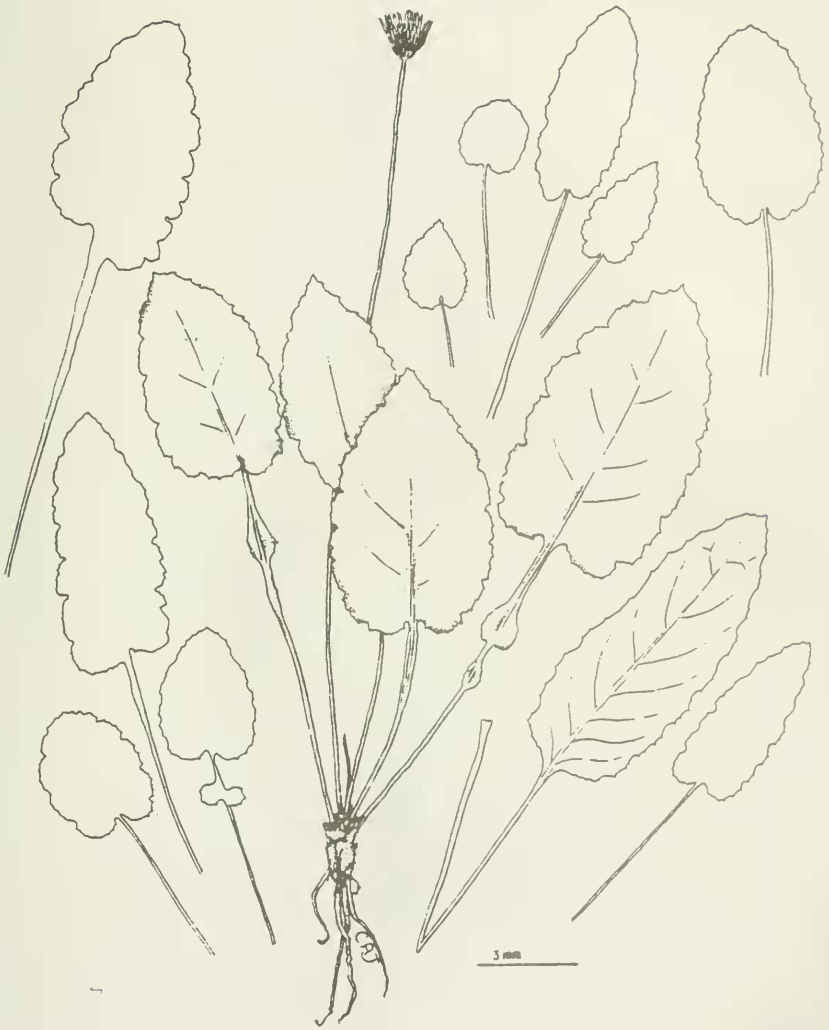


Figure 5. Habit and leaf variation of *Chaptalia hintonii* (*Hinton 8562*). Disconnected leaves show species variability at × 2/3 scale of full plant.

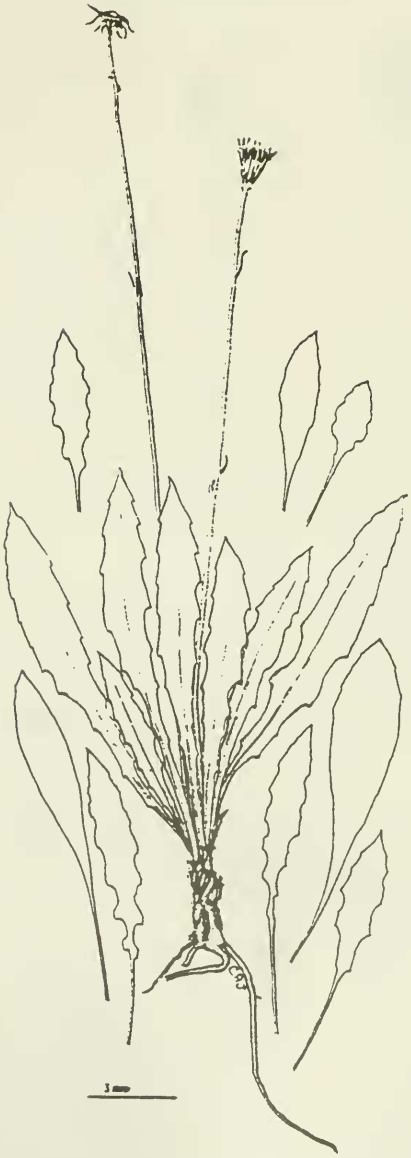


Figure 6. Habit and leaf variation of *Chaptalia pringlei* (*Nesom 4405*). Disconnected leaves show species variability at × 2/3 scale of full plant.

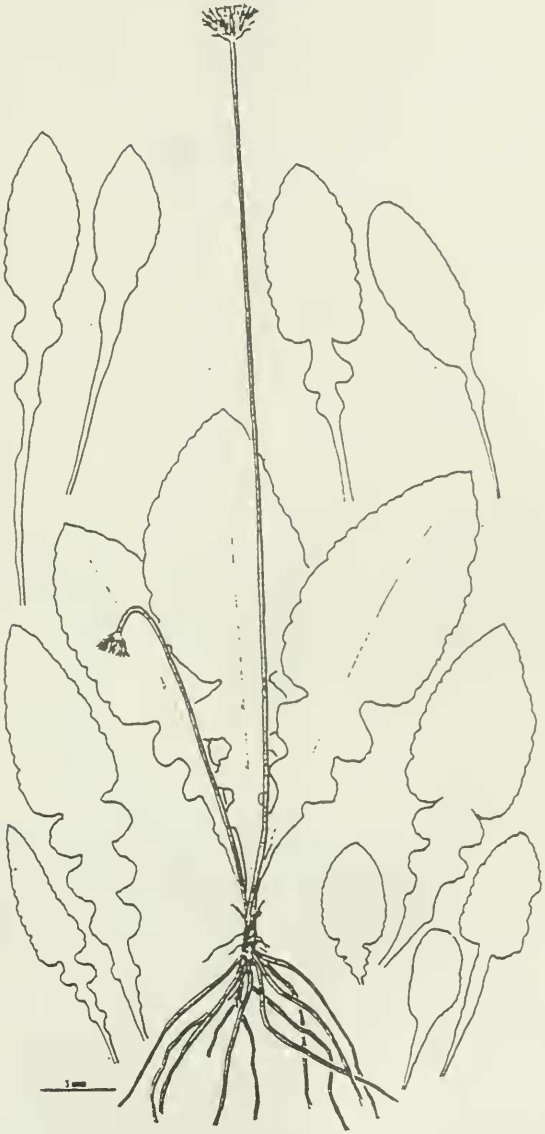


Figure 7. Habit and leaf variation of *Chaptalia nutans* (*Ventura A. 12763*). Disconnected leaves show species variability at × 2/3 scale of full plant.

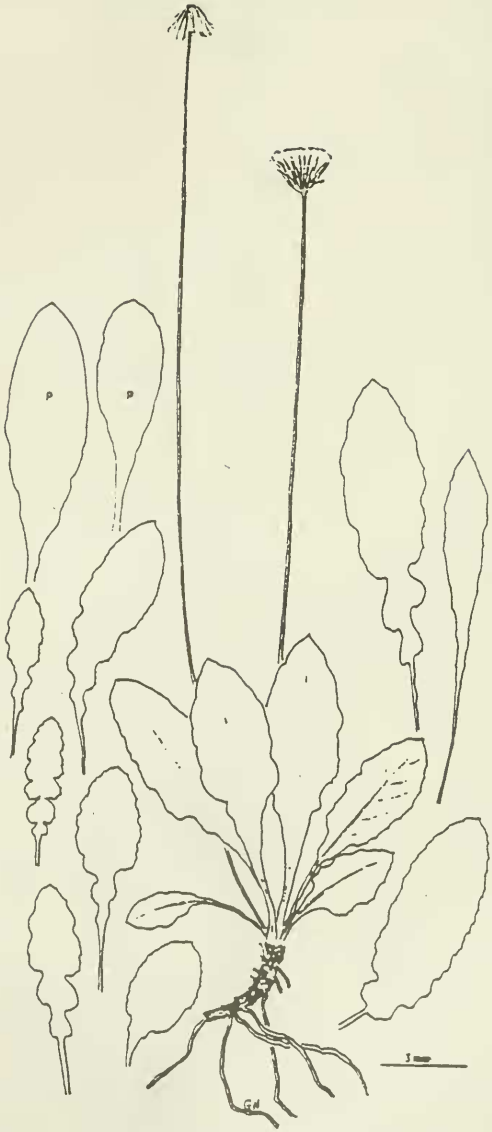


Figure 8. Habit and leaf variation of *Chaptalia texana* (*Nesom 4758-B*). Disconnected leaves show species variability at × 2/3 scale of full plant. Leaves marked "P" are from *C. petrophila*.

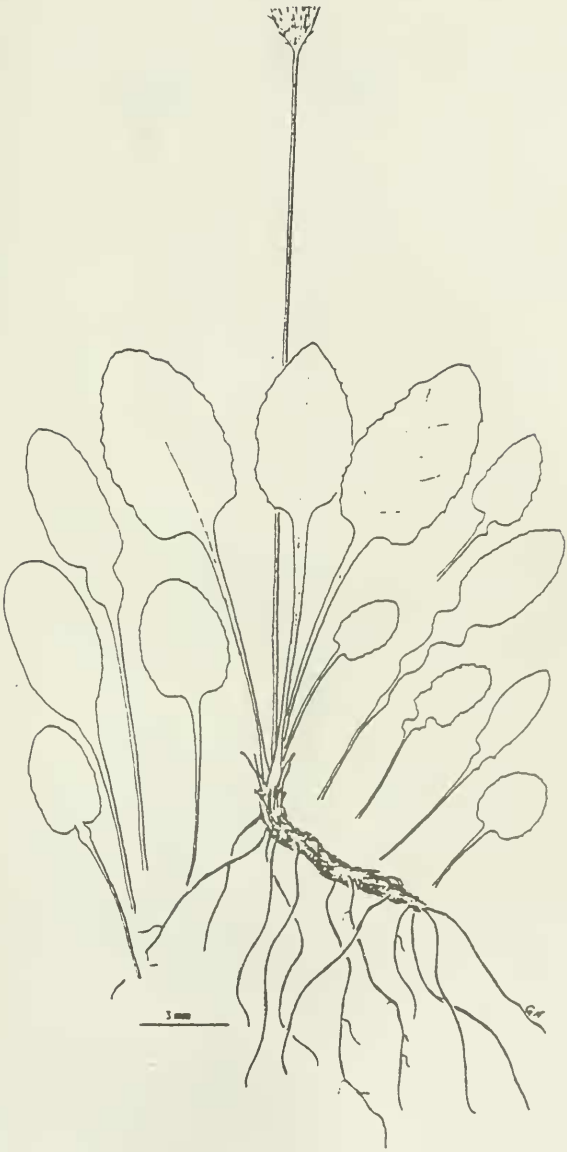


Figure 9. Habit and leaf variation of *Chaptalia transiliens* (*Nesom 4759*). Disconnected leaves show species variability at × 2/3 scale of full plant.

Figure 10. Habit and leaf variation of *Chaptalia hololeuca* (*Palmer 298*). Disconnected leaves show species variability at × 2/3 scale of full plant.

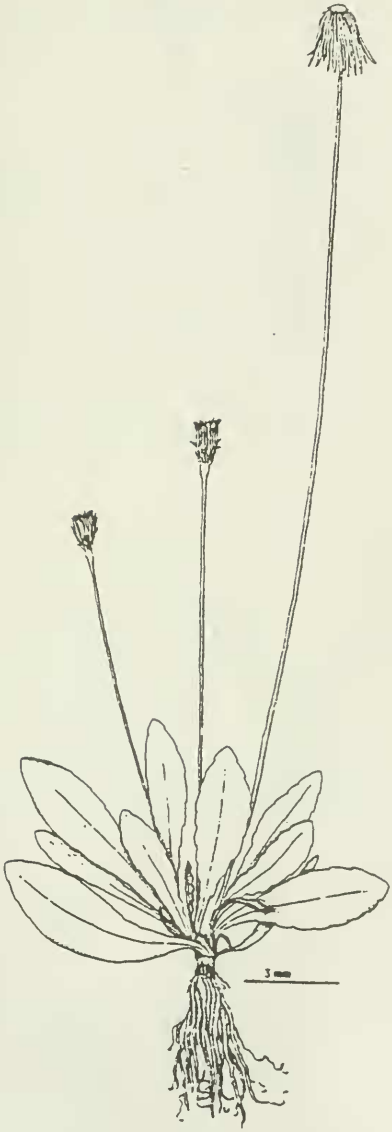


Figure 11. Habit of *Chaptalia albicans* (*Ventura A. 8381*).

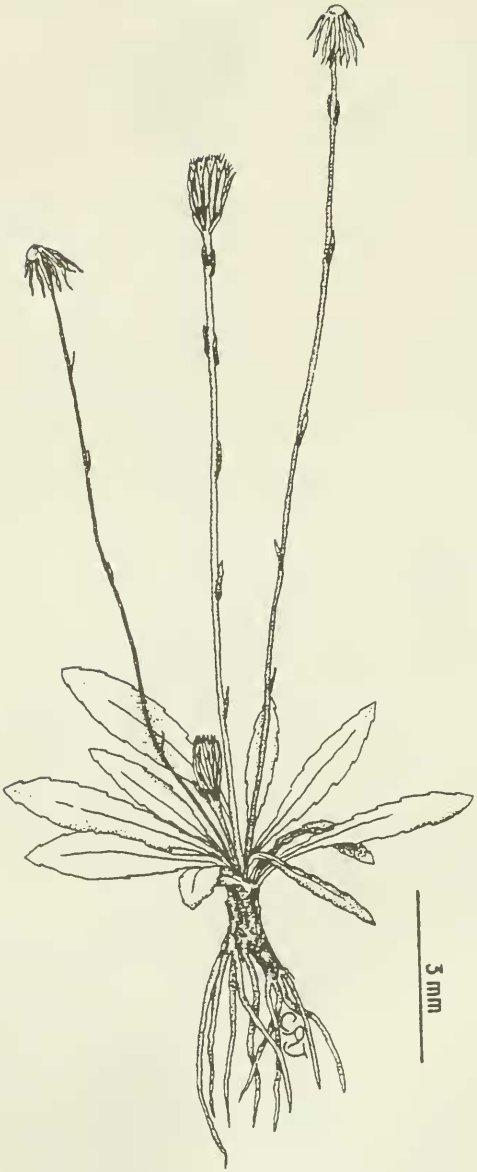


Figure 12. Habit of *Chaptalia runcinata* (*Nesom 4439*).

(HOLOTYPE: OXF ex herb. Lambert, marked by Pavón as "*Hieracium stipitatum* N.E.", photo-US!).

ACKNOWLEDGMENTS

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